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THE CHROMOSOME HYPOTHESIS OF LINKAGE APPLIED TO CASES IN SWEET PEAS AND PRIMULA

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THERE are two views as to the nature of linkage. The earlier view, developed by Bateson and his co-workers, is that this phenomenon is an expression of symmetrical reduplications in the germ tract. A more recent view, developed by Morgan and his co-workers, treats linkage on the basis of a linear arrangement of genes in the chromosomes and of the history of these genes during normal gametogenesis. The advocates of the reduplication view have rarely applied their principles to the results on *Drosophila* on the ground that the results for *Drosophila* are complicated by sex-linkage. That sex-linkage is simply an additional, but wholly independent, phenomenon, is proven by the many cases in *Drosophila* in which sex-linkage is not involved, yet in which the linkage of the genes to each other is of the same type as the linkage of sex-linked genes to each other.

In this paper I shall attempt to show that the theory of linkage which we have successfully applied to all cases in *Drosophila*, whether involving sex-linked genes or genes which show no sex-linkage, applies equally well to the non-sex-linked cases occurring in sweet peas and primula. The only serious drawback to such an application lies in the nature of the data which have been collected for these cases. The least satisfactory form of data from which to determine a linkage value is that presented by F_2 results. In cases in which two recessives enter from opposite parents ("repulsion"), the excessive smallness of the double recessive class in F_2 renders any calculation subject to great error. Slightly better are the F_2 results from coupling,

but here there is no direct parallelism between the zygotic and gametic ratios. In determining what gametic ratio underlies the F_2 results given by an experiment, the practise has been to compare by the eye the given result with a series of F_2 results calculated from selected gametic ratios. Collins has shown¹ that this practise has led to serious error. In F_2 coupling cases in which there has been no crossing over in one sex (autosomal genes in *Drosophila*), there is a *direct* relation between the gametic and zygotic series, but only in certain classes which comprise from one fourth to less than one half of the individuals of an experiment. While such data are more accurate than the usual F_2 results, yet the percentage of individuals which can be used directly is so low that we avoid the use of such a method. In F_2 results involving only sex-linked genes, the efficiency is at least 50 per cent., for here there is always a direct relation between the gametic and zygotic ratios in one half the flies (the males). However, half the total number of flies (the females) are useless unless the cross is made in such a way that F_2 becomes a back cross. These different kinds of F_2 results (the two most advantageous of which are not generally applicable) are separated in effectiveness by a wide gap from the back cross which we use equally well in all cases, which gives a zygotic ratio directly proportional to the gametic ratio, and in which *every* individual occurs in the most advantageous relations.

Perhaps the least unsatisfactory method of dealing with such F_2 series as are available in the case of the sweet peas, is by means of the coefficient of association as derived by Yule. Yule's coefficient of association is calculated from a zygotic series of the form $AB:aB:Ab:ab$ by the formula:

$$\text{Coefficient of association} = \frac{(AB \times ab) - (aB \times Ab)}{(AB \times ab) + (aB \times Ab)}.$$

To find the gametic ratio corresponding to this coefficient, use is made of a table which gives the coefficients

¹ AM. NAT., '12.

calculated from the zygotic series corresponding to such gametic ratios as 2.5:1, 3:1, 3.5:1, etc. For the same ratio in the coupling and repulsion series the coefficients are slightly different, so that two tables should be made.

Upon the chromosome basis the best method of expressing the amount of linkage is in terms of percentage of crossing over. The gametic ratio $n:1$ found through the coefficient of association, when expressed as a percentage

becomes $\frac{100}{n+1}$.

According to the chromosome hypothesis, all genes which are linked to each other lie in the same chromosome. In sweet peas the first case in which linkage was observed was that of round pollen² and red flower color. Later it was found that hooded standard was linked to round and to red. The genes for these three characters, then, may be treated as though carried by the same chromosome, which we may call chromosome I, of the sweet pea.

The relative distances of these genes from one another in the chromosome can be determined from the degrees of linkage. The farther apart in the chromosome any two genes lie, the greater will be the amount of crossing over between them. If two genes lie very close together, then the percentage of crossing-over will be very small (the gametic ratio very large).

Fortunately Punnett has recently collected the data upon these linkage cases in sweet peas. In the table which follows, I have summarized the data given by the various tables of Punnett. In the first column to the right of the data appear the coefficients of association. In the next column appear the corresponding gametic ratios calculated by interpolation to the nearest tenth. In the last column are the equivalent percentages of crossing over, found from the gametic ratios.

We may use one per cent. of crossing over as our unit of distance in measuring the space between two genes.

² I have used a terminology here like that used for the cases in *Drosophila*, naming the gene after that member of the pair of allelomorphs which may

The gene for red is then about eleven units from that for round, and the gene for hooded is nearly one unit from that for red.

TABLE I
CHROMOSOME I

Round Pollen and Red Color						
Wild Type	Round	Red	Round Red	Coefficient of Association	Gametic Ratio	Percentage of Cross-overs
Coupling ... 7,897	583	614	2,197	.9596	7.9:1	11.2
Red Color and Hooded Standard						
Wild Type	Red	Hooded	Red Hooded			
Coupling ... 2,568	16	17	857	.9998	125.:1	.8
Round Pollen and Hooded Standard						
Wild Type	Round	Hooded	Round Hooded			
Coupling ... 626	74	83	174	.8932	4.7:1	18.
Repulsion ... 3,140	1,413	1,438	14	.9577	8.7:1	10.3

The order of arrangement of these genes in the chromosome can be discovered from a comparison of the linkage values found above. The linkage value (11.2) for round and red is the most accurately determined of those involved, so that we may lay this down as our initial or base line:

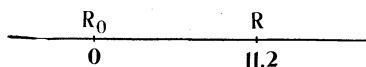


DIAGRAM I. R_0 = round pollen, R = red flower.

The next most accurate value is that for red and hooded, namely, 0.8. Hooded lies therefore only about one unit from red, but if these two values only, namely, round red and red hooded, were given, we should be unable to decide whether hooded lies between round and red at a position near 10 (that is, $11.2 - .8$) or beyond red in a locus at 12 (that is, $11.2 + .8$). In order to determine whether hooded lies to the left or to the right of red the data for the third value, round hooded, need only be accurate enough for us to decide between these values of 10

and of 12 units. The data from the coupling experiments (which even though less extensive than those from the repulsion experiments are probably more accurate) give a value of about 18 units. Since the repulsion data give 10 units, 18 is probably too high, and an intermediate position correct. The higher (12) of the two possible values is then the correct value. The position at 10 is not excluded by these data, but is far less probable. In a case in which one of the two first values is very small, as here, the accuracy demanded of the remaining or third value is much greater than in cases where neither of the values are small, and one has only to decide between two very different values by aid of the third. There are other ways of arriving at this order of genes which are independent of the size of the values. One of those methods, such for example, as that of double crossing over, would definitely settle the order of these three genes, but unfortunately such data have not yet been published.

If hooded lies beyond red at 12, the complete first chromosome diagram will be as follows:

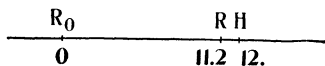


DIAGRAM II. Chromosome I, Sweet Pea. R_0 = round pollen, R = red flower, H = hooded.

In the above diagram R_0 indicates the locus of round (and also of long). The symbols in the diagrams are used to designate loci which may be occupied by either allelomorph of the pair.

It has been observed that hooded flowers have always a uniform color in standard and wings, instead of having these two regions colored differently as in the normal or bicolor type. Bateson assumed that this unicolorism was only another somatic effect of the hooded gene. However, an alternative explanation is that the unicolor is caused by a specific gene which is very closely linked to hooded. If this should be found to be the case, then this fourth gene also will be located at about 12 units from round.

There is one other gene which probably belongs in the first chromosome, namely, the intensifier found in the "black knight" race. The linkage data of red color and intensity of color have been given in Report II to the Evolution Committee, page 90.

TABLE II

Red Color and Intense Color						
Wild Type	Red	Intense	Red Intense	Coefficient of Association	Gametic Ratio	Percentage of Cross-overs
Coupling ... 149	29	35	22	.527	1.9:1	35.

If these data are significant, then intense is in the first chromosome at a locus about 35 to the right or left of red. It should give about 24 (35 — 11) or 46 (35 + 11) per cent. of crossing over with round, depending on whether it lies about 24 to the left of round or 35 to the right of red.

THE SECOND CHROMOSOME OF SWEET PEAS

In the case of the second chromosome in sweet peas, the linkage values are based on smaller numbers, but the order of genes is more certain.

The first linkage case of this chromosome was that of sterile anthers and light axils. Later the cretin form of flower was found to belong to this linkage group. As in the case of the first chromosome, I have summarized the tables of Punnett in Table III.

TABLE III

CHROMOSOME II

Sterile Anthers and Light Axil						
Wild Type	Sterile	Light	Sterile Light	Coefficient of Association	Gametic Ratio	Percentage of Cross-overs
Coupling ... 1,170	41	30	379	.9945	22.:1	4.4
Repulsion ... 1,335	643	714	2	.988	20.:1	4.9

Light Axils and Cretin Flower						
Wild Type	Light	Cretin	Light Cretin			
Coupling ... 282	49	52	59	.734	2.6:1	28.
Repulsion .. 48	22	27	3	.610	2.7:1	27.

Sterile Anthers and Cretin Flower

	Wild Type	Sterile	Cretin	Sterile Cretin		
Coupling ...	165	58	58	78	.556	2:1 33.
Repulsion ..	764	355	345	25	.683	2.6:1 28.

The linkage value for sterile and light, namely, 4.4 units, is the most accurately determined of those in the second chromosome. The value for light and cretin is about 28 units. Using the distance 4.4 between sterile and light as our base line, then, we should find that cretin lies at $4 + 28$ or 32 from sterile if the order of genes is sterile, light, cretin; but if the order is cretin, sterile, light, then cretin should lie at $28 - 4$ or 24 from sterile. The value for sterile cretin should approximate either 24 or 32. There is no very small value here as there was in the first chromosome, and not such great accuracy is required of the remaining value, since it should be easy to distinguish between 24 and 32. The coupling data for this value gives 33 units, which enables us to fix the order of genes as sterile, light, cretin. The following diagram of chromosome II expresses these relations more clearly.

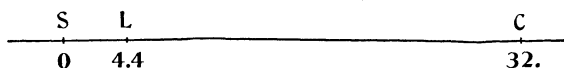


DIAGRAM III. Chromosome II, Sweet Pea. S = sterile, L = light, C = cretin.

When crossing over is as free as in the case of sterile and cretin and of light and cretin there should be some double crossing over. That is, crossing over might occur in the section of the chromosome near sterile and light and at the same time another crossover could occur in the section between light and cretin. This occurrence would be readily seen if normal plants heterozygous in any combination of these three genes were back-crossed to plants purely recessive in all three. A relatively few plants from such a test would give very valuable information on several points, while an experiment of a few thousand individuals from such back-cross tests would enable one to discover, through the phenomenon of interference, much

as to the character of the chromosome, the average length of the internode, and the percentage of chiasmata per node.

INDEPENDENCE OF CHROMOSOMES I AND II OF SWEET PEAS

If two groups of genes are carried by separate chromosomes, we may expect to obtain free assortment and typical 9:3:3:1 ratios in F_2 , when any two genes from different groups are involved. There are rather extensive data for three such cases in sweet peas, and in each there is practically complete independence. The data given in Table IV are summarized from Report III to the Evolution Committee (page 37) and Report IV (page 17).

TABLE IV

INDEPENDENCE OF THE FIRST AND SECOND CHROMOSOMES

Round Pollen (1st) and Light Axil (2d)						
Wild Type	Round	Light	Round Light	Coefficient of Association	Gametic Ratio	Percentage of Cross-overs
1,246	341	399	142	.131	1.15:1	47.
Red Color (1st) and Light Axil (2d)						
Wild Type	Red	Light	Red Light			
1,563	545	506	232	.136	1.16:1	47.
Red Color (1st) and Sterile Anthers (2d)						
Wild Type	Red	Sterile	Red Sterile			
838	403	265	147	.071	1.07:1	48.

The greatest departure from the 50 per cent. of crossing over expected from independent assortment is only to 47 per cent.

There are several other characters whose genes seem to be independent of those in the first and second chromosomes. This is interesting from the point of view that each independent gene or group of linked genes requires a distinct chromosome as a carrier.

LINKAGE CASES IN PRIMULA

In the case of primula, linkage was first found between red (versus green) stigma and red (versus magenta) flower color. Long style (versus short) and dark stem (versus light) were found to be linked with red stigma. Indications were observed that still a fifth gene, a dominant which reduces the color of the flower to a tinge in the corolla tube, belonged to this group.

A back cross involving the three genes, red stigma, red flower and long style was made. Credit is due to Gregory for the use of this method for obtaining linkage data. Unfortunately many of the individuals were useless for the linkage of red flower color, because of the occurrence of white; and the numbers are small.

In Table V, I have summarized the data given by Gregory.⁴

TABLE V
THE FIRST CHROMOSOME OF PRIMULA

Red Stigma and Red Flower							
	Non-crossovers		Crossovers		Coefficient of Association	Genetic Ratio	Percentage of Cross- overs
	Red Stigma Red Flower	Wild Type	Red Stigma	Red Flower			
Coupling							
back cross	28	39	17	18		1.9:1	34.6
	Wild Type	Red Stigma	Red Flower	Red Stigma Red Flower			
Coupling F ₂	1,174	305	289	232	.511	1.8:1	35.3
Red Flower and Long Style							
	Non-crossovers		Crossovers				
	Red Long	Wild Type	Red	Long			
Coupling							
back cross	40	53	6	5		8.4:1	10.9
	Wild Type	Red	Long	Red Long			
Coupling F ₂	38	2	4	12	.966	8.6:1	10.4
Red Stigma and Long Style							
	Non-crossovers		Crossovers				
	Red Stigma Long	Wild Type	Red Stigma	Long			
Coupling							
back cross	44	64	35	30		1.6:1	37.

⁴ *Jour. Genetics*, '11, Vol. I; *Proc. Roy. Soc.*, '11, Vol. —, 84.

Red Stigma and Dark Stem						
	Wild Type	Red Stigma	Dark	Red Stigma	Dark	
Repulsion	137	66	62'	0	--	--

The three values are—red stigma red flower 35, red flower long style 11, and red stigma long style 37. Of these, red stigma red flower is based upon the most data, and may therefore be taken as our base line. The value for red stigma long style should be $35 - 11$ or 24, if the order of genes is long, red stigma, red flower; but $35 + 11$ or 46, if the order of genes is red stigma, red flower, long. The value shown by the table is 37. This means that long lies to the right of red at a locus 46.

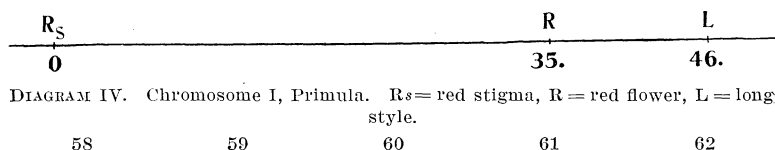


DIAGRAM IV. Chromosome I, *Primula*. R_s = red stigma, R = red flower, L = long style.

The apparent discrepancy between the values 46 and 37 is due in most part to double crossing over, the effect of which is always to lower large values disproportionately more than short. When the discrepancy is known, the amount of double crossing over can be calculated approximately. Here the amount of double crossing over is

$$\frac{46 - 37}{2} = 4.5.$$

That is, 4.5 per cent. of all the gametes are the result of double crossing over. A somewhat larger amount of data from a back cross in which all the individuals are effective would give by direct experiment a true value for the amount of double crossing over.

A chromosome diagram should be built up of values independent of double crossing over. According to our experience with *Drosophila*, if there is not more than ten per cent. of crossing over between two genes, the double crossing over is negligible. Thus in the first chromosome in sweet peas, the values obtained from the experiments are not changed by double crossing over. However, in the

case of the second chromosome, where the total percentage of crossing over is about 32, there is probably one or two per cent. of double crossing over. The diagram of the second chromosome is in this respect only tentative, and the plotted position of cretin will be moved a little farther to the right when the amount of double crossing over between light and cretin has been found. The value 4.4 for sterile anther light axil is not affected by double crossing over, since the section of chromosome between these two loci is so short that a double break would probably not occur between them at all. The amount of double crossing over between any two loci can only be found when there is a gene between them. Thus if a gene should be found which lies between light and cretin, either by indirect calculation or, better, by direct experiment, the amount of double crossing over could be found. The more genes which can be worked with in the same chromosome, the more accurate becomes the diagram.

All the values found for these cases in sweet peas and primula are based upon such small numbers that they can be used only as illustrations of the way in which one would apply to new cases certain principles worked out in *Drosophila*. While they serve as examples in line with these principles, they are entirely inadequate as proof. A very interesting case of variation in linkage is presented by some of the families involving chromosome II of the sweet pea. In this article I have avoided such data as far as I could, but it is possible that the order in which I have aligned these genes will be found to be incorrect when data upon all three genes in a back cross are obtained. Such data would show, through the phenomenon of double crossing over, what the order of genes is, even though variations in the linkage should occur.

COLUMBIA UNIVERSITY,
May, 1914